SPAWNING BEHAVIOR AND SEXUAL DIMORPHISM IN FUNDULUS HETEROCLITUS AND ALLIED FISH.

(CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORIES OF THE UNIVERSITY OF MICHIGAN. NO. 108.)

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INTRODUCTION.

Of recent years much stress has been laid upon the structural basis of behavior, especially among the lower organisms. Among the higher animals, on the other hand it has long been understood that function and structure are simply dynamic and static phases of the same thing. There would be little excuse for the present paper, then, unless it should serve to show that these ideas of structure and function — sexual dimorphism and spawning behavior — have a far wider application than has commonly been supposed. It will be shown that even minute, temporary structures, that have previously escaped the eye of the investigator, are as truly adaptations for spawning as are the more obvious secondary sexual characters, such as differences in the sizes of fins, in color pattern, in body form, etc.

My attention was first called to this subject by chance. One day early in the summer of 1906, while engaged in cross-breeding species of *Fundulus* at the Marine Biological Laboratory of Woods Hole, I was fortunate enough to observe the spawning act in the species *Fundulus heteroclitus*. These fish were spawning in a small aquarium and in a good light so that the entire process could be observed in minute detail without difficulty. Afterwards I was fortunate in being able to observe the spawning of *Cyprinodon* under equally favorable conditions. These observations led to a closer study of the behavior of these species and to a consideration of their sexual dimorphism as the structural basis of this behavior. The other two available species of *Fundulus*, *F. majalis* and *F. diaphanus* were then brought in for purposes of comparison.

The wash drawings reproduced in Plates XXVII. and XXVIII. were made under my direction by Miss Ella Weeks of the State Agricultural College of Kansas. I take this opportunity of expressing my appreciation of the quality of her work and my indebtedness to her for her service. I also wish to express my thanks to Professor Jacob Reighard for his helpful suggestions and criticism.

The plan of the paper is to treat each species separately, to give a summary of the main points, and to conclude with a general discussion of the origin and significance of the structure and behavior described.

The four species dealt with all belong to the family Pœciliidæ (the killifishes). The following statements referring to sexual dimorphism in this family are quoted:

"Sexes usually unlike, the fins being largest in the males, but in some species the females are much larger in size. Many of the species are ovoviviparous, the young well developed at time of birth. In these species the sexes are very unlike, the anal fin of the male being developed into an intromittent organ."—Jordan and Evermann, "Fishes of North America," p. 631.

"In many species the sexes are dissimilar, the female being larger and less brilliantly colored, with smaller fins."—"Cambridge Natural History."

I have been unable to find anything in the literature concerning the spawning behavior of these species.

For purposes of clearness it seems best to present the facts on spawning behavior before those on sexual dimorphism, since behavior throws so much light on the significance of structures.

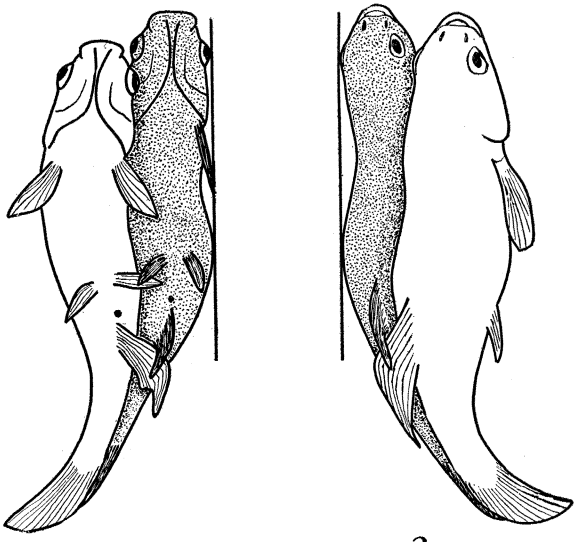
Fundulus Heteroclitus (Linn.).

(Common Killifish; Mudfish; Cobbler; Mud Dabbler; Mummichog.)

Spawning Behavior.

The spawning act proper was the first to gain my attention and it is hardly likely that I should have noticed it had I not been slightly familiar with Professor Jacob Reighard's unpublished observations on the spawning habits of certain inland species. In spawning the male clasps the female firmly around the slender portion of the body just back of the dorsal and anal fins, using as claspers his large, strong anal and dorsal fins. The two fins

of the male slip in under the homologous fins of the female, which are raised up to admit them, and nearly surround the body of his mate. The ventral fins of adjacent sides are also locked in similar fashion. The female is usually forced against some perpendicular solid object such as a stone, a mass of seaweed or the glass sides of the aquarium — most frequently the latter when in captivity. When the female is thus seized by a male she suddenly assumes a characteristic attitude, the whole body, when observed from above having the conformation of a somewhat flattened S, the head being pressed against the solid, that part



TEXT PLATE I. Showing the spawning attitude of male and female Fundulus heteroclitus, the female darkened.

FIG. 1. Ventral view, showing the position of anal and ventral fins.

FIG. 2. Dorsal view, showing the position of dorsal fins. This view is a half side view. The straight line indicates the points of contact with a solid substance such as the glass sides of the aquarium. ½ natural size.

of the body just back of the head being bowed outwards and not touching the solid surface, the region of the abdomen being again against the solid, and finally the whole tail region being free from the solid and bent sharply away from it and slightly upwards (see Text Plate I.). In this rigid position she is supported from the bottom by means of her anal fin, which

extends nearly at right angles from the belly and is thick and stiff and well adapted for supporting the weight of the two bodies and often becomes much inflamed by frequent contact with the bottom. The male, clasping the female firmly as he does, holds his entire body against hers for from one to two seconds. While in this position a quivering vibration of the posterior half of the bodies of both fish occurs, during which eggs and sperm are extruded in very intimate contact with each other. Whether this vibratory movement is initiated by one or both sexes I cannot say for certain, but I am inclined to believe that the female only is responsible, the male simply remaining passive and taking up the vibration from the female. My reasons for believing that such is the case are: first, the vibratory rhythm of the two fish spawning together is always in perfect unison, which would hardly be the case when two fish of very different sizes clasp; second, I have often seen females assuming the spawning attitude and going through the vibratory movement when there were no males in the vicinity.

This spawning act is highly adaptive in several respects:

1. The vibratory movement serves to extrude ripe eggs and ripe sperm at the same instant. It is only in this way that the sexual products can be extruded as is shown by the fact that the females are forced to adopt this method of relieving themselves when there are no males present.

2. The position assumed by the two sexes is such that eggs and sperm are extruded in very close proximity and could scarcely fail to come in contact. Chances of failure are minimized by the fact that on the one hand the milt is shot out with considerable force directly at the eggs as they are extruded, and on the other the eggs exert a strong chemotactic influence upon the sperm, which I demonstrated by the following experiment. A freshly stripped egg was put on a glass slide with a few drops of water and then a drop of sperm was put in the water at a distance of half an inch. In a very short time the egg was surrounded by a dense cloud of sperm and inside of two minutes all of the sperm was seen to be gathered about the egg. In addition to this the surface of the egg is very glutinous and probably holds all sperm that comes in contact with it.

3. The position of the anal fin of the female is such that it supports the weight of both fish, the distal end of the fin being in contact with the bottom which under natural conditions is usually composed of soft mud. Since this fin receives the vibratory movement of the body it necessarily stirs up a considerable amount of mud and also makes a shallow depression. The eggs, as soon as they are extruded, fall to the bottom and either settle in the small hole or are at least partially concealed by the settling mud. That some such protection is necessary is shown by the fact that the fish themselves are very fond of their own eggs, devouring them eagerly when they can be seen. This curious type of cannibalism was observed repeatedly in aquaria where the bottom was free from mud. The females were the chief offenders in this respect although young males occasionally devoured the freshly extruded eggs. It was a very common sight to see other females rush up and seize the eggs as soon as they were extruded. Frequently, however, females were observed to turn and devour their own eggs. This destruction of eggs probably occurs only to a very limited extent under normal conditions for the reasons cited above.

Courtship, Rivalry and Display.

As might be expected, the male takes the more active and aggressive part in courtship but the female frequently displays herself in such a way and assumes such postures as are calculated to attract the male. Females laden with very ripe eggs frequently display themselves by turning on their sides near the bottom, and spurning the latter with their tails, thus causing their silvery white bellies to flash in the light. This, I noticed, seldom failed to attract the males if there were any of the latter about. This curious flashing movement is by no means restricted to the females of this species, but was observed occasionally in the males of the same species, in both sexes of *Fundulus majalis*, and in several other marine species. It was, however, especially noticeable in actively spawning females and seems to be of undoubted service in attracting males.

When both sexes are at the height of their sexual activity there is little that could be termed courtship. The females are

burdened with their great masses of eggs, that must distend their adbomens uncomfortably, and are eager to get rid of their burdens. This can most easily be accomplished by contact with the males, but may be and frequently is accomplished without the latter. The females usually, however, retire to the bottom and place themselves in contact with some solid object, sometimes only the snout being actually in contact, thus assuming a position in which they may be most readily clasped by the male. Whenever a male sees a female in this position he loses no time in spawning with her. If a female after taking up the position just described is not joined by a male she is very apt to relieve herself by assuming the S-shaped posture characteristic of the spawning act and by vibrating her body just as she would if clasped by the male. The eggs are thus plentifully extruded, but if no males are present, they are not and probably never can be fertilized. If, however, any males are in the vicinity they are always attracted by the vibratory movement and dart toward the source of vibration.

Courtship, if such by courtesy it may be called, occurs shortly before the sexual climax. Fish in this condition swim about comparatively quietly in pairs, the female above and the male just below and slightly back of her. This position enables him to see her more readily and at the same time to guide her about by gently butting her on one side or the other with the top or sides of his head. I have observed very many pairs swimming about in this way for considerable periods of time. Gradually the male becomes more excited in his movements and the preliminary courtship merges into spawning behavior proper. At first the attempts at spawning on the part of the male are apt to consist merely of efforts to corner the female and to induce her to seek some retired spot at or near the bottom. To accomplish this he rises from beneath her and butts her downwards with the sides of his head. If he succeeds in driving her into a suitable place he attempts to spawn with her, the first few trials lacking the vigor characteristic of ruling males. Sexual excitement increases rapidly so that before many minutes have passed the male is apt to be seen spawning promiscuously with any female that he encounters. This transition from courtship to spawning was ob-

served both in aquaria and under natural conditions. In the open, excited males were often seen to be in rapid pursuit of the females, succeeding occasionally in cornering and clasping them. The pursuit of the males was often so impetuous that the females were entirely frightened away. The coyness on the part of the females acts as an excitant on the males.

Rivalry among the males is very keen and as a rule those whose "spawning plumage" is most brilliant succeed in driving away all competitors. I have observed under normal conditions that a certain male, always the most brilliantly colored one in the neighborhood, seems to control the situation, driving away all males that attempt to encroach upon his territory. The size of the male seems to be a much less important factor in determining his success than is the degree of sexual maturity as indicated by the brilliance of his coloration, for I have often seen a male of comparatively small size put to rout several others of twice or three times his size, such is the impetuosity of his attack. I was able to observe this rivalry to better advantage in aquaria where it was possible to identify the various individuals and thus to keep an accurate record of the success or failure of each male. The following record was made on June 20, 1906.

A fresh lot of *F. heteroclitus* was placed in the aquarium early in the morning. At about ten o'clock in the forenoon they were observed to be actively spawning. About twenty females were spawning on the bottom of the aquarium on the side away from the light. Seven males seemed ready to take part in the process, but one very large male, more brilliantly colored than the rest, continually drove away all other males that attempted to spawn. So solicitous was he about driving off his competitors that he could scarcely attend to all of the females that were ready to spawn. While the ruling male was engaged in clasping one female another male in a remote portion of the aquarium would occasionally succeed in spawning with another female. Whenever such an occurrence was observed by the ruling male, he always gave chase and invariably routed the intruder. This male was so much larger and more vigorous than any of the others that none dared to dispute his authority to the extent of offering battle. For purposes of experiment I removed this male from

the aquarium and put him in a smaller vessel by himself, being careful to keep him out of the strong light. When thus removed from the sexual environment, he almost immediately underwent a very marked change in appearance, becoming decidedly lighter in color, and inside of ten minutes losing all of the steely blue glint that is so characteristic of sexual excitement. Putting a dark colored fish in a strong light causes a similar lightening of color, but that the change in question was not due to light seems certain for all strong light was excluded. As soon as this ruling male had been removed the other males usurped his prerogative and a struggle for supremacy immediately ensued. The combat between the six remaining active males was for a time very evenly waged, since there was no great disparity in size, but after about ten minutes a single male, and he not the largest, had gained supremacy and had succeeded in driving away his rivals whenever they approached. Occasionally one of the outsiders plucked up sufficient courage to challenge the ruling male and a combat ensued. The males fight with their heads and mouths, butting one another fiercely and accasionally locking jaws and struggling like dogs. When a male wishes to challenge he approaches rather cautiously, body trembling with excitement and all fins extended to the utmost, presenting as formidable an aspect as possible. The male thus challenged adopts a similar attitude and rushes at his foe with alacrity. Curiously enough the male that has once gained supremacy always emerges victorious from these contests, and the defeated male retires into hiding until he has regained sufficient courage to challenge again. After about half an hour the large male that had been removed to another vessel was returned to the aquarium. At first he seemed to take no interest in the spawning activity going on about him, but gradually he aroused himself and made an occasional half-hearted attempt to clasp a female that came near him and advertized by her attitude her desire to spawn, but he was always rudely interrupted and put to rout by the new ruling male, which although of very much smaller size, attacked with such vigor that his much bulkier opponent was forced to retire. By degrees, however, the large male increased in vigor, at the same time growing darker and reassuming the blue glint that he had so quickly

lost. In about twenty minutes he was as dark and as brilliant as before and had succeeded in ousting the usurper from his domain, although not without repeated struggles in which his victory became more decisive each time. The next day the same male was in control, but on the following day another male of medium size had acquired supremacy. It is probable that the period of sexual climax is of short duration, not exceeding three or four days. A male at the very height of his sexual activity is afraid of nothing and is practically invincible.

This account will serve as a sample of the scenes observed repeatedly in the aquaria and in natural conditions during the months of June and July. The last recorded observation of spawning in this species was taken on July 7, although ripe males and females were found for at least two weeks later.

This account of the spawning behavior of *Fundulus heteroclitus* may well be concluded with an account of a few more experiments and some additional isolated observations.

Experiment 1. — A considerable number of actively spawning males and females were separated into two aquaria, the males in one and the females in another. Inside of about fifteen minutes the males had all become nearly as pale as the females and spent their time in wandering about uneasily as though seeking for a place of escape. The females, on the other hand, seemed to be very little affected by the absence of the males but went on extruding eggs as freely as if the males had been present. It is probable that the initial stimulus to egg extrusion given by the males lasted some time after the removal of the latter. The eggs were always eagerly devoured either by the female that laid them or by another that rushed up and siezed them before she could turn around. It is hardly probable that eggs are so eagerly devoured in the open, as the food supply is not restricted as in an aquarium.

Experiment 2. — An aquarium was prepared with mud and stones on the bottom to approximate natural conditions, and in it were placed five spawning fish of each sex. These fish, instead of appearing to enjoy their new surroundings, lost all interest in spawning and spent all of their time in exploring their environment. In the meantime the males lost all of their "spawning

plumage" and became decidedly pale. The females too seemed to have forgotten about spawning in their anxiety to become familiar with the new neighborhood. On the following day the fish were still uninterested in spawning and I concluded that they had passed the sexual climax while they had been busy with their explorations.

Experiment 3. — I put several males that had been isolated for several days into an aquarium containing only females. These had been extruding eggs at intervals, but as soon as the males appeared, they seemed to become excited and immediately began to take up spawning attitudes and to extrude eggs in much increased amounts. It seems certain that the presence of the male, even when the latter refrains, as in this case, from any participation in the spawning act, exercises an exciting influence upon the female. The stimulus is probably a visual one, for the appearance of the male is very characteristic.

Additional observations:

1. Occasionally pairs were observed to come together and spawn in open water without being in contact with any solid. It was also not unusual to see them spawning against the bottom instead of against some more or less perpendicular object.

2. On three occasions I observed a female following a male around and apparently endeavoring to incite him to spawn with her by bumping him and placing her body in contact with his. On one occasion she succeeded in inciting him to clasp her for an instant. This assumption of the initiative on the part of the female struck me as being decidedly abnormal and may have been a perversion of instinct, due to confinement.

3. I observed that females that were being guided about by the males occasionally seemed to resent this infringement upon their liberty and engaged in a somewhat mild form of contest with the males, returning their butting in kind. The male, however, invariably seemed to have his way in the end.

4. On June 27, I observed *F. heteroclitus* spawning in the Eel Pond in the shadow of a boat and in about eighteen inches of water. The males would chase females out beyond the shadow but usually returned quickly to the shade. I have noticed repeatedly that the fish prefer the darker places for spawning.

5. After watching the spawning of this species in the open, I believe that large males, when at the height of their sexual period, control considerable areas in the Eel Pond and elsewhere. Although an active male may pursue a female or another male for considerable distances he soon returns to the neighborhood over which he seems to exercise authority. This phenomenon is by no means unusual in fish.

Sexual Dimorphism.

The following passages, refering to sexual dimorphism, are selected from Jordan and Evermann's systematic account:

". . . fins moderate, the dorsal inserted in males midway between snout and tip of caudal; in females farther back; oviduct attached to anterior ray of anal fin for one-half to two-thirds its length; . . . Coloration in males dark dull green, the belly more or less orange yellow; sides with numerous quite narrow, ill-defined silvery bars made up of silvery spots, most distinct posteriorly; besides these are numerous conspicuous white or yellow spots, irregularly scattered; vertical fins dark with numerous small round pale spots; dorsal often with a blackish spot on its last ray; anal and ventrals yellow antertiorly; under side of head yellow; young males with alternate bars of dark and silvery, the former becoming in time the ground color, the dorsal ocellus more distinct. Females nearly plain olivaceous, lighter below, without spots or bars, the scales finely punctate; sides often with about fifteen dark crossbars or shades. Young, especially young females, with more or less distinct dark cross bands; these always present in the very young, in females narrower than the interspaces, in males much broader and less numerous."

This description, while accurate enough so far as it goes, needs to be supplemented with regard to certain details. It also fails to take into consideration the fact that there are marked seasonal changes not only in color but in the actual size of certain parts such as belly and fins, and in the production of certain temporary organs in the male.

First of all I would like to supplement Jordan and Evermann's account and to call attention to certain points. Then I shall be in a position to discuss the seasonal changes.

The description of the male is fairly accurate for one out of the breeding season. I wish, however, to call attention to the relatively large size of the dorsal and anal fins of the male as compared with those of the female (see Plate XXVII., Figs. 1 and 2).

The enormous difference in the fin coloration of the two sexes should also be emphasized, those of the female being almost devoid of pigment while those of the male, although more deeply colored in the spawning season, are always markedly pigmented, the pigment being laid down is such a way as to produce a mottled pattern. The posterior and proximal half of the dorsal is, however, always much darker than any other area on the fins and is the equivalent of the much more distinct spot seen on the dorsal of male *Fundulus majalis*. There is also a marked difference in the shape and in the strength or stiffness of these fins in the two sexes. In the male there is a pronounced posterior prolongation of both fins, especially the anal. These fins are stronger and better provided with muscle in the male than in the female and hence are better fitted for clasping organs.

Discussion of the Seasonal Changes.

The seasonal changes may be classified as follows:

In the female:

1. Paling of the general body coloration.

2. Distension of the abdomen with eggs and consequent lessened activity.

3. Thickening and inflammation of the anal fin.

In the male:

1. Intensification of pigmentation in definite regions.

2. Acquisition of a steely blue gleam in the scales of certain regions. (1 and 2 are spoken of collectively as "spawning plumage.")

3. Development of certain temporary organs on the scales that I have chosen to call "contact organs."

1. The paling of the general body coloration in the female and the intensification of pigmentation in the male might be attributed to the opposite metabolic conditions prevailing in the two sexes at this period. The female, having to sacrifice so much of her vitality for egg production, must have a lowered somatic metabolism, the index of which is the diminished production of pigment. The male, on the other hand, seems to have much excess vitality, since the production of sperm is far less taxing on somatic vitality than is the production of eggs. The deposition of pigment here

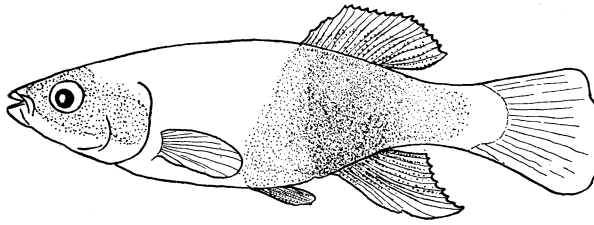
is probably an index of a very rapid metabolism that expresses itself in other ways such as greater activity, greater courage, and in the production of excrescences, etc.

2. The thickening of the anal fin in the female may be partially a phenomenon of inflammation produced by irritation. The sources of irritation are twofold. In the first place the tip of the fin is rubbed violently against the bottom during the spawning act. In the second place the frequent expulsion of eggs through the tubular extension of the oviduct that runs down the posterior ray of the fin, probably causes inflammation in this and adjacent parts. The thickening of the fin gives a firmer support for the spawning pair than would the fin in its usual condition, and in addition stirs up the mud more effectively as has been shown.

3. The steely blue gleam so characteristic of spawning males, reminds one of iridescence but is not of the same character. The blue color is probably due to a combination of chromatophores and iridicytes. The former are extremely extensible in that the pigment is capable of flowing out over a wide area through slender, branching canals. The latter are extremely minute prismatic crystaline bodies that serve the purpose of refracting the light. They evidently lie above the chromatophores which furnish the absorbing background. In some way the colors at the red end of the spectrum are absorbed by the melanin and the combined colors of the violet end of the spectrum are reflected as the steely blue gleam. The extension and contraction of the melanophores seems to be a reflex closely associated with sexual excitement, and may be considered as a sort of involuntary flush.

4. The structures that I have chosen to designate as contact organs, occur as finger-like processes on the margins of all the scales in certain regions, and upon the fins that are used in clasping. The appearance of these processes is well shown in the photographs reproduced in Text Plate III.

It is of interest to note that contact organs occur only on actively spawning males and only upon those parts that are in contact with the female during the spawning act and upon the top and sides of the head, parts that are used for butting the female in courtship and one another when fighting. The distribution of the contact organs in the four species studied is represented in



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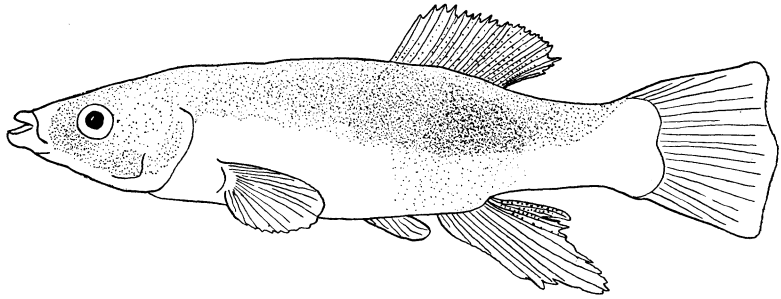

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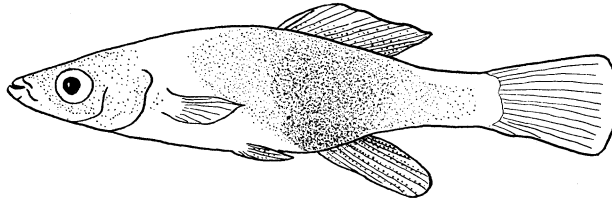

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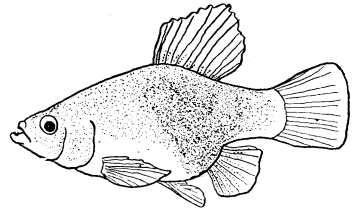

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TEXT PLATE II.

Showing the distribution of contact organs in males of the four species. The stippled areas represent regions supplied with contact organs. Where the stippling is heaviest the contact organs are most numerous and best developed. The dots on the fins represent contact organs.

1. *Fundulus heteroclitus.*
2. *F. majalis.*
3. *F. diaphanus.*
4. *Cyprinodon variegatus.*

Text Plate II. It is also interesting to note that the best developed and most frequent contact organs occur where the pressure in spawning must be the greatest, namely between the dorsal and anal fins and on these fins at or near their bases. In each case the maximum distribution seen in the males collected is shown in the figure. The stippling is closer in regions where the contact organs are thickest and best developed, and more open where the latter are more scattering and less well developed. No attempt has been made in these diagrams to represent actual numbers or sizes.

TEXT PLATE III.

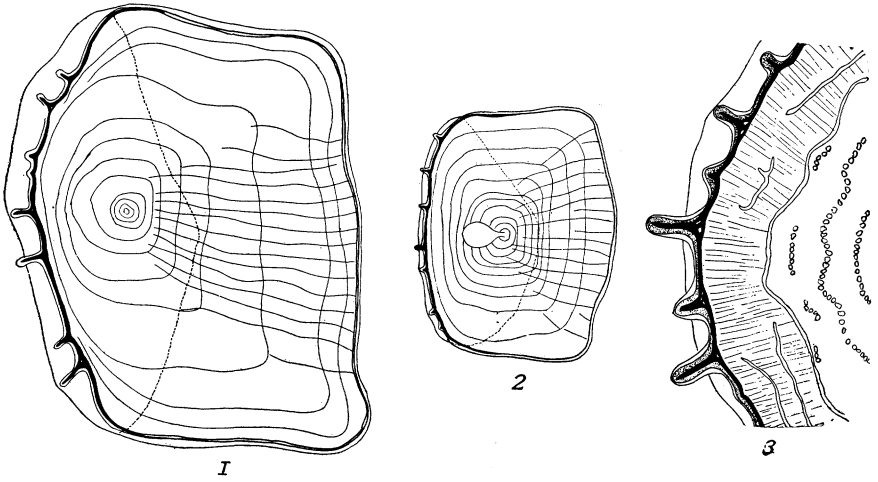
Showing scales with contact organs, × 12.

1. Scale from the side of a large male *F. majalis*.
2. Scale from a corresponding part of the body of a large female *F. majalis*.
3. Scale from the lateral line region between the dorsal and anal fins of a spawning male *Cyprinodon variegatus*.
4. Scale from a similar location of a spawning female *Cyprinodon variegatus*.

An examination of a considerable number of males reveals the fact that only those in spawning plumage possess contact organs,

while some of these possess them only on the top or sides of the head. It is my belief, although I am not at present in possession of any direct evidence on the subject, that the organs are developed antero-posteriorly, either in response to a fixed law of development or because there is an earlier need for these structures on the cheeks and on the top of the head, since these parts are used in the preliminary courtship, coming into frequent contact as they do with the body of the female.

The contact organs are practically alike in all of the species studied, although they vary slightly in form and in size relative to that of the scale on which they occur. They are best developed



TEXT PLATE IV.

Camera drawings of typical scales from the region between the dorsal and anal fins of spawning males.

1. *Fundulus heteroclitus.*

2. *F. diaphanus.*

3. Enlarged detail drawing of a portion of the exposed margin of a scale taken from the side of a male *F. majalis.* The black region represents the horny margin of the growing region of the scale that is prolonged into spikes that support the contact organs. The stippled area represents the dermis. The clear outside area represents the epidermis. The striated portion is the non-calcified portion of the scale.

in *Fundulus majalis*, but are simply larger here than in the species under consideration. Photographs and camera drawings (see Text Plates III. and IV.) show clearly the appearance of the contact organs in typical scales taken from males of the four species.

They consist first of a core of horny material or sclerified connective tissue (see Text Plate IV., Fig. 3), that arises like a sharp spike from the free growing edge of the scale. This skeletal support is represented in black in the drawing although in life it is nearly transparent. Various stages in the development of the spikes may be seen both in the detail and in the general drawings. They first appear as slight outwardly directed folds of the edge of the growing region of the scale, and gradually assume the spike-like form. Outside of this horny support there is a fairly thick layer of dermis, represented in the detail drawing in stippling. The histological characters of this layer I have been unable to make out in the formalin preserved specimens that have been my only resource in the present paper. Outside of the dermis there is a thin layer of epidermis that is often found worn off at the tips of the papillæ, allowing the horny spike to protrude.

The contact organs do not lie flat against the body of the fish, but stand out at an angle of about thirty degrees, so that they can readily be seen in profile with the naked eye. This attitude is decidedly advantageous for giving a rough surface or for a sensory function. Probably the former function is the principal one, although I am not sure that the latter function is not subserved. If the contact organs should prove to be sensory we can understand how their stimulation by the vibration of the female during the spawning act might account for the extrusion of sperm on the part of the male. These points have not been made out on account of the lack of histologically fixed material, but a study of the histology and function of these organs will furnish material for a more special paper.

It should be stated that the contact organs are possibly related to the so-called "pearl organs" found in other species of fish. Their structure, however, is entirely different in that they are chiefly dermal in origin and possess the horny spike-like support, while pearl organs are little more than epidermal callouses.

The resemblance of the contact organs to the teeth on the margin of ctenoid scales will probably strike the reader. It has occurred to me that here we have the origin of the ctenoid type of scale. Ctenoid scales are found on the most highly specialized of our Teleosts but are described as being absent in more primi-

tive families such as the one with which we are dealing. Is it not possible that we have in this family ctenoid scales developed as mere temporary structures, used only by the males during the spawning season? If we admit the possibility of this condition we can see how such structures might become permanent, be produced in both sexes and subserve another function.

FUNDULUS MAJALIS.

(Killifish; Mayfish; Rockfish.)

Sexual Dimorphism.

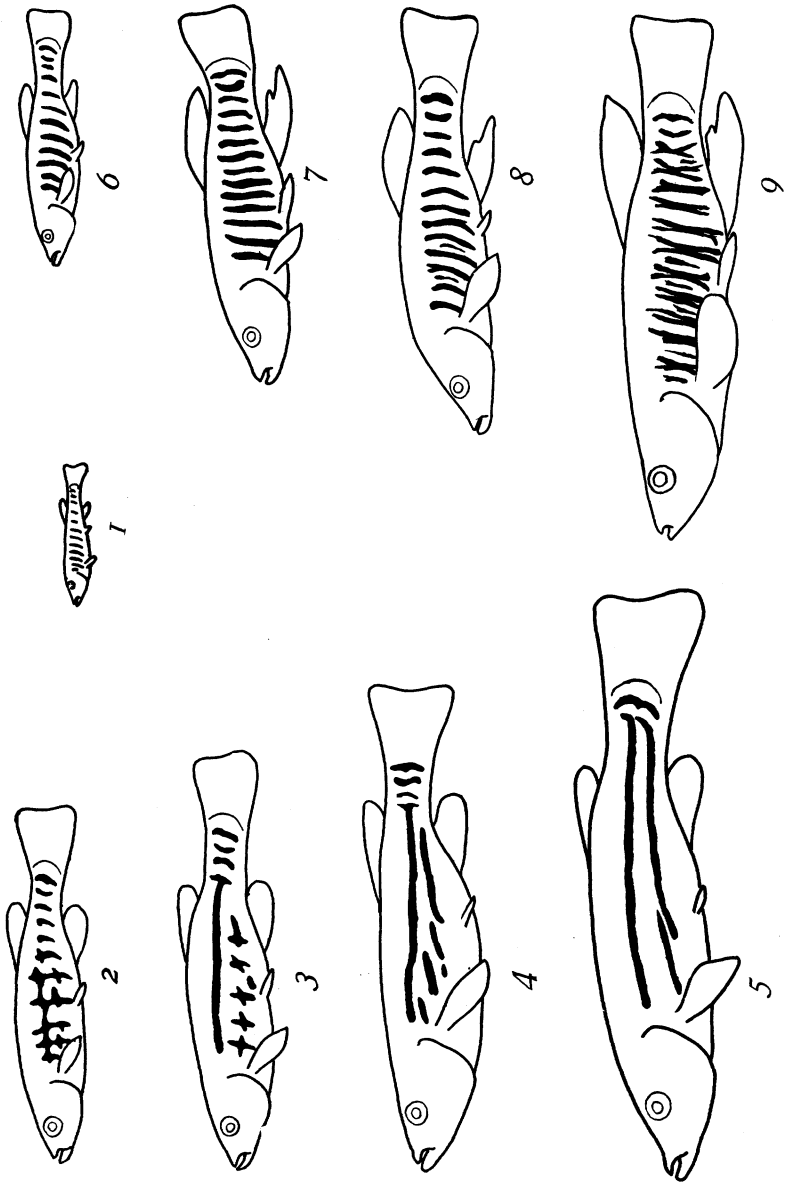
The following passages, referring to sexual dimorphism, are selected from Jordan and Evermann's account:

". . . anal fin very high in males, moderate in females; ventrals long in the males, reaching past front of anal; . . . Males dark olivaceous above; sides silvery or somewhat golden, with about a dozen broad transverse bars of the color of the back; posterior part of the dorsal fin with a black patch; fins yellowish or pale. Females olivaceous above, white below, a narrow black longitudinal stripe along sides about on the level of the eye and as wide as the pupil; below this two similar black stripes anteriorly and one posteriorly, the upper one being interrupted; one or two black bars at the base of caudal. Females usually larger than the males. A large male of this species, in high coloration, taken at Beaufort, N. C., showed the following colors in life: Back olive, sides and belly bright salmon yellow; lower fins clear yellow; pectorals and anals with some dusky; posterior edge of caudal dark; dorsal nearly all black, a large black ocellated spot on the last rays; opercles and under parts of head with an inky suffusion; cheeks, top of head, and mouth bronze yellow; sides with about eighteen narrow, dusky vertical bars."

The "high coloration" referred to in the Beaufort male is undoubtedly the "spawning plumage" and, although a somewhat more highly colored condition is described than I have observed in any male at Woods Hole, the account is probably entirely accurate for the species in more southern waters. The males that I have observed (see Plate XXVII., 4) have the back and the upper part of the sides almost black instead of olive as described; lower part of the sides and belly orange or golden yellow instead of salmon yellow; dorsal, anal and caudal fins golden with a tendency toward dusky, the dorsal being only a trifle darker than the other fins instead of being black as described above;

cheeks top of head, etc., heavily shaded with a bluish-black coloration, reminding one of the blue glint of the male *F. heteroclitus* instead of bronze yellow as described. The black spot on the posterior rays of the dorsal may, as in the illustration (Plate XXVII., 4), be composed of a series of spots arranged in a sort of circle. This is more apt to be the case in very large specimens.

The color pattern of both sexes is gradually modified during the lifetime of the individual and all stages in the production of the complete adult pattern are readily found. The young of both sexes are always cross barred somewhat like the adult male, but the bars are less numerous, numbering seven to ten as compared with from fourteen to twenty in adults. The increase in number of bars takes place by means of a longitudinal splitting of individual bars and by the appearance of small new bars between the old ones (see Text Plate V., Figs. 8 and 9). In the former case the two bars produced by the division of one simply spread apart and at the same time broaden out; in the latter case the small alternate new bars merely increase in size until they become nearly as large as the original bars, although it is usually easy to distinguish the latter by their greater length. In one unusually large male I observed fourteen well developed bars nearly all of which had begun to split at the ends as though preparing to double the number of bars once more. As a rule the most anterior bars are the first to show signs of splitting, the tendency proceeding antero-posteriorly. It seems to be a very general rule that meristic changes of this sort proceed in this direction. The color pattern of the females is at first similar to that of the young male, but during the second season, probably, a marked change begins to take place. The eight or ten bars that exist at that time show decided irregularities in outline, each bar, beginning with the most anterior, sending out at two places forward and backward processes, which, on examination, prove to be arranged in two longitudinal lines, the upper one on a line with the eye and the lower one on a line with the angle of the operculum (Text Plate V., Fig. 2). The processes especially those of the upper bar, continue to elongate anteriorly and posteriorly until those of adjacent bars fuse together into a continuous longitudinal stripe, the remaining portion of the bars becoming attenuated and



TEXT PLATE V.

Showing stages in the development of the adult male and female color pattern in *Fundulus majalis*. These are camera drawings made from formalin preserved specimens except in two cases 1 and 9 which are taken from free-hand drawings of living fish. ½ natural size.

1. A young fish of undetermined sex, showing the type of pattern seen in all young fish.

2 to 5. Stages in the development of the female color pattern. The gradual change from cross bars to stripes is clearly brought out.

6 to 9. Stages in the development of the most specialized male color pattern seen in 9. Not many males reach this stage.

gradually fading out (Text Plate V., Fig. 3). The lower line of processes behaves in a slightly different manner. Instead of spreading out to form a continuous straight band it forms a series of short, nearly longitudinal bars (Text Plate V., Fig. 4). Later on these short bars fuse end to end in various fashions to form from two to five longer bands or stripes one of these extending nearly two thirds of the length of the body and the others, some above and some below the lower long stripe, vary greatly in length in different individuals (Text Plate V., Fig. 5). This process of conversion of bars into stripes takes place, as in the case of the doubling of bars in the male, in an anteroposterior direction. In half grown females all stages of the process may readily be found. Such specimens show from two to five of the posterior bars intact while the stripes at the anterior end are well marked. I have never yet seen an adult female in which all of the bars had disappeared, the most posterior one always persisting. The appearance of adult females is strikingly characteristic and must serve as a very efficient recognition mark for the males. The sexual difference is accentuated by the fact that the fins of the female are nearly or quite devoid of any dark pigment, only a small amount of a light yellowish pigment being present and that chiefly on the caudal fin.

The fins of the male bear the same characteristics as do those of *F. heteroclitus*, but are even more pronounced in their sexual dimorphism. Especially is this the case in the anal fin which is prolonged backward more markedly than in the previously described species (see Plate XXVII., Fig. 4). The anal fin of the female is swollen and inflamed in egg-laden specimens freshly brought in. The flow of milt is free and copious only in males possessing the highest coloration. The contact organs are even better developed than in *F. heteroclitus* and their distribution is very similar.

Beyond these indications I have no direct evidence bearing on the spawning behavior of *Fundulus majalis*. Although taken in large numbers when they were apparently at the height of their sexual activity, as indicated by the abundance of ripe eggs and sperm, they showed no tendency to spawn in captivity. The fish are much wilder than *F. heteroclitus* and seem to feel captivity much more keenly. All of their normal activities seem to be, for a time at least, inhibited by confinement in restricted

quarters, as is indicated by the fact that they will not feed until they are nearly starving, so it is hardly to be expected that they would spawn under these conditions. I think there can be no reasonable doubt, however, that their spawning behavior closely resembles that of the species described, especially since the observed behavior of a representative of another genus, viz., *Cyprinodon variegatus*, so closely resembles that of the latter. It is highly probable, judging by the very much elongated anal fin of the male *F. majalis* that this fin plays a more important part in clasping the body of the female than does the analogous fin of *F. heteroclitus*, but the difference, like that in the other details of spawning behavior, is probably one of degree rather than one of kind.

Fundulus Diaphanus.

The following extracts, referring to sexual dimorphism, are taken from Jordan and Evermann's systematic account:

"Fins not large; dorsal and anal rather low; ventral scarcely reaching vent in females; somewhat longer in the males. General color olivaceous; sides silvery. Male with about 20 silvery vertical bars, narrower than the dark interspaces; female with 15 to 20 transverse bars, shorter than the silvery bands of the male, the interspaces pale; back sometimes spotted; young always with black bars; fins nearly plain."

In the above description the dark coloration is arbitrarily spoken of as the background on which are superimposed silvery bands, in the case of the male. In the case of the female, on the other hand, the silvery is referred to as background for the somewhat narrower dark bars. A casual examination of the figures representing the two sexes (Plate XXVIII., 1 and 2) will show, I believe, that the dark bars are analagous in both male and female, those of the former simply being considerably broader and a little darker than those of the latter. This greater distinctness of the cross banded pattern in the males is just what we should expect to find if we compare this with the other species examined. The dimorphism in color pattern, however, has not become so pronounced in this case as in the others, and probably represents a more primitive condition.

The dimorphism in the case of the dorsal and anal fins, although not nearly so marked as in the other species, is still quite evident,

especially in the case of the anal, which is considerably longer in the male. That of the female, as in the other species, is stiff and swollen, but only in the basal two thirds. The dorsal of the male is frequently colorless or nearly so, like that of the female, but is often decidedly mottled with dark pigment after the fashion seen in the male of *F. heteroclitus*, but much more lightly. The chief mottling is found on the posterior rays, a sort of prophecy of the very marked spots on this fin in other species. The contact organs are similar in form and distribution to those of *F. heteroclitus*.

In general it might be said that this species shows the beginnings of sexual dimorphism in practically all of the points that become so marked in other species, and probably represents a primitive condition.

I am sorry to be unable to present any facts regarding spawning behavior, but must plead as an excuse that this species, being a fresh or brackish water form found in a large pond on Martha's Vineyard, was inaccessible for observation in its natural haunts, and could be transported to aquaria only with the greatest difficulty. Moreover, when once they are transported and are safely housed they die off very rapidly and the diligent collector receives a poor reward for his labor. The species is not at all resistent to adverse conditions as is *F. heteroclitus* or even *F. majalis*.

The presence of a sexual dimorphism, the same in kind although different in degree, from that in other species of the same genus, lends probability to the belief that the spawing behavior is similiar to that described above.

CYPRINODON VARIEGATUS Lacépède.

(Sheephead Minnow; Purcy Minnow; Short Minnow.)

Spawning Behavior.

The opportunity was not afforded me of observing the behavior of this species in its native environment, but I was very fortunate in being able to get fairly complete records of its spawning habits by the use of aquaria.

The following observations were made on July 20:

A medium-sized aquarium was fitted up with stones *Ulva*, *Fucus*, etc., to approximate natural conditions, and five male and

nine females of the species *Cyprinodon variegatus* were introduced. At about eight o'clock in the morning, when all was quiet in the room I had a fine opportunity of observing the spawning behavior of these fish. Of the five males three were in spawning plumage. one of them being noticeably more brilliant than the other two. When I first observed these fish this brightest male had acquired complete control of the situation. He was so extremely active and pugnacious that he succeeded in driving not only the other males but the females into the friendly shelter of the masses of coarse brown seaweed. Whenever any of the other fish so much as ventured to poke its head out of the shelter the ruling male would dash up and scare it into its retreat again. One of the brighter males, less subdued than the rest, ventured out more frequently and farther than the others. Instead of meekly retiring before the vigorous onslaught of the enemy, he offered considerable resistance. On several occasions the encounters between the two males developed into combats at close quarters, in which heads and jaws were the weapons. They would begin by butting heads fiercely and would occasionally grasp jaws and shake one another powerfully from side to side as though each were endeavoring to tear out his opponent's jaw. These struggles were usually short lived, one of the belligerents, invariably the one that had been in hiding, seemed to tire. They would then separate, as though by mutual consent, and the defeated male would ingloriously retreat to shelter, usually slowly as though exhausted. I have been unable to notice that either of the combatants in these frays receive any injury.

It is, I believe, more of a test of vigor and endurance than any attempt to inflict bodily injury. On the supposition, then, that sexual vigor and general bodily vigor run parallel and that the index of both is the brilliancy of coloration, we can readily understand why it is that the most brilliantly colored male is invariably the victor in these struggles for supremacy. It probably is the case too that a higher courage accompanies a higher bodily and sexual tone and makes a male at his climax practically invincible. It seemed to me, as I watched the activities of this male, that his extreme impetuosity was decidedly a detriment to him, for he defeated his own ends by driving away all females that ventured

to seek the open. The ruling male always approached these females, which were ready to spawn, judging by their distended abdomens, with so much fierceness and speed that they were forced to retreat. Occasionally this male succeeded in cornering a female in one of the angles of the aquarium either at the bottom or at the sides, and spawned with her. The method of spawning is not unlike that observed in *Fundulus heteroclitus*. The male holds the female just forward of her caudal fin, using chiefly his very large, strong dorsal fin for this purpose. He lies slightly on the back of the female, but mainly side by side with her. The anal and ventral fins are used to hold the female up against the clasping dorsal, but these fins do not, so far as I was able to observe, clasp so firmly as in *Fundulus*. The approximation of sexual openings is not nearly so close as in the last-named species and hence there is probably less surety of successful fecundation. The eggs and sperm are, however extruded in such close proximity that the chances of failure are comparatively slight. While clasped by the male the female vibrated the body as described for *Fundulus* but more rapidly. In fact the whole spawning act is of such short duration that it is extremely difficult to see exactly what takes place. One has to make repeated observations, watching each detail of the process and even then some details elude ones most careful scrutiny.

July 22. — Two days later the ruling male still continued to rule although challenged frequently by the other male, now almost equally brilliant. The encounters between these two belligerents was very interesting, reminding one of nothing so much as an encounter between two game cocks. They approach threateningly, every fin erected and body quivering for the fray. Then they dash at one another, the ruling male being slightly more aggressive. After an encounter, much more evenly waged than on the former occasion, the rival male gives up temporarily and retires to his corner. He is still full of fight, however, for in a few moments he begins to make threatening demonstrations in his corner, turning sudden summersaults and making quick, active darts out and back. This behavior never fails to bring his opponent to the fray again. This sort of thing usually lasts until one of the combatants — always the lesser male — grows weary and

retreats to a convenient hiding place, there to recuperate for another series of encounters. Several other fairly brilliant males could be made out, hiding in the same fashion. The females are still too frightened to emerge from shelter. The fierce aspect of these fighting males is remarkable in creatures so small. When swimming ordinarily the dorsal fin is not used, being kept folded flat on the back. But whenever fighting or sexually excited, this fin comes into action, expanding like a bat-wing sail.

The reckless courage of the ruling male surprised me. I put into the aquarium a male *Fundulus hereroclitus* of large size. Without a moment's hesitation the little warrior dashed up to the far bulkier intruder and caused the latter to beat an ignominious retreat. Several larger fish of other species met a similar reception and fate.

July 23.— On the following day the ruling male had been deposed and there was an extremely vigorous struggle for supremacy among the other males. Only one of these failed to enter the lists. This one had as yet not reached the sexual climax and was, consequently *hors du combat.* As one might have anticipated, the male that had ousted the original ruling male was the victor, the others finally acknowledging defeat by retiring to shelter. The same program was then repeated that has been described for the previous days.

The deposed male now showed signs of waning vigor in the paling of his "plumage," which was becoming rather dull at the posterior end of his body. This fading out of brilliancy proceeds in a postero-anterior direction, the top of the head being the last part of the body to lose its bright coloration.

July 29.— Both males and females of *Cyprinodon* are seen to have passed the sexual period. The females are no longer distended and no longer show any fear of the males, the two sexes mingling quite amicably. The males have all lost their spawning coloration except for traces of iridescent green about the head. The dorsal fin of the males, having lost most of its pigment, shows in one or two cases quite a noticeable dark spot on the posterior rays. This spot is, however, not nearly so distinct as that in the females. In color the males are now pale green with dusky markings that stand out somewhat more clearly now that

the iridescence and general dark body coloration has nearly disappeared. The males are still greener than the females but the difference in the intensity of the coloration is far from marked.

When the fish were fed it was noticeable that the males always erected the dorsal fin when they made a dash for a fragment of food. They seem to raise this fin whenever excited in any way.

Sexual Dimorphism.

The following extracts referring to sexual dimorphism are taken from Jordan and Evermann's systematic account:

"Body very short and robust, in adults high and much compressed, the females abruptly constricted at the base of the caudal peduncle. . . . Dorsal fin moderate, in females as high as the length of its base, in males much higher; origin of dorsal midway between base of caudal and end of snout; base of fin $1\frac{1}{3}$ to $1\frac{2}{5}$ in length of head; longest ray (in male 2 inches long) reaching half way from base of fin to base of caudal, the anterior rays equaling length of head and extending beyond tips of posterior rays when the fin is depressed; in females the longest ray about $1\frac{1}{2}$ in head; origin of anal under eighth or ninth ray of dorsal, the fin very small and much higher than long; length of base about equaling snout; longest ray half length of head (less in females). No external oviduct. Caudal truncate or slightly emarginate, $1\frac{1}{4}$ in head; ventrals, in adult males, reaching in front of anals, $2\frac{1}{3}$ in head; in females reaching vent; . . . Scales large, tuberculate in males, arranged in regular series; . . . Color: Male olivaceous; from dorsal forward above pectoral to head deep, lustrous steel blue, the color very intense and conspicuous in life; rest of upper parts with rather greenish luster, becoming dull slaty blue, and on cheeks, opercles, sides anteriorly and belly deep salmon color; lower lip and preopercle violet; dorsal blackish, the anterior margin of fin orange; caudal dusky olive with jet-black bar at tip, and a narrow black cross-streak at base; anal dusky at base, bordered entirely around with bright orange; ventrals dusky, bordered with orange; pectorals dusky orange, darker below. Smaller specimens show some orange shading on the sides, and sometimes also traces of the cross-bands of the female. Female very light olive; lower half of the sides with about 14 alternately wide and narrow vertical, dark bars, those anteriorly narrower and closer together; usually 7 or 8 dark cross-bars on the back, alternating with the wide bars below; these bars are of various degrees of distinctness, sometimes almost obsolete; a dusky area below eye; young with broad greenish cross shades wider than the interspaces; belly pale or yellowish; lower jaw largely blue; cheeks brassy; dorsal dusky, with an intense black, faintly ocellated spot near tip of last rays; caudal faintly reddish, with a black bar toward base; other fins pale orange, with some dark points. Length: Male 3 inches; female

2 inches. Cape Cod to the Rio Grande, in brackish waters, entering streams, very abundant southward, the males more highly colored southward, but the southern form (called *gibbosus*) not otherwise different."

These sexual differences, especially those of general bodily form, comparative size and shape of fins, color pattern, etc., are well brought out in the illustrations (Text Plate II., Figs. 3 and 4). Characters involving color, iridescence and the like cannot be represented in monocrome, so it will be necessary to fall back upon verbal description. For this purpose I cannot do better than to refer to Jordan and Evermann's full account for details not brought out in the illustrations. This account was evidently written with reference to the fish when in "spawning plumage," no reference being made to the fact that, in the males especially, the color and iridescence are merely temporary adornments, characteristic of the breeding season alone. Before and after the breeding season the males are about the same color as the females — perhaps a trifle greener.

The points of sexual dimorphism to be especially born in mind are the following:

1. The male is usually somewhat larger than the female — the opposite being the case in the species of *Fundulus* described.

2. The male, in "spawning plumage," is very much more brilliantly colored than the female.

3. The body of the male is decidedly deeper but more compressed than that of the female, differing from *Fundulus* in this respect.

4. The dorsal, anal and ventral fins are larger in the male than the female, even more markedly than in *Fundulus*.

5. The cross-barred color pattern is retained more nearly intact in the female than in the male, the opposite condition holding for *Fundulus*.

6. The dark, ocellated spot, that, in *Fundulus* characterizes the posterior rays of the dorsal fin of the male, is present here only in the female, although the same area in the male is usually more heavily pigmented than the rest of the fin in the male.

7. The contact organs are similar in form and distribution to those of *Fundulus*.

8. As in *Fundulus*, all of the fins of the male are more deeply and more brilliantly colored than in the female.

9. The generally aggressive and warlike aspect of the male is in striking contrast to the comparatively mild and timid aspect of the female. This contrast is more striking in *Cyprinodon* than in the species of *Fundulus* examined.

10. This exceedingly fierce aspect of the male is largely due to the very marked height of the dorsal fin and his method of carrying it spread to the utmost.

Summary and Conclusions.

Classification of Secondary Sexual Characters.

I. Of the permanent differences the following is a list:

1. Relative size of the sexes.
2. General body form.
3. Relative sizes of the various fins.
4. Shape of the various fins.
5. Color pattern (*a*) on the body, (*b*) on the fins.
6. Quality and intensity of coloration, whether it consists of pigmentation or of iridescence.
7. Relative abundance of the sexes.

II. Of the temporary differences that appear only during the spawning season the following is a list:

1. The distended abdomen of the female.
2. The swollen and inflamed anal fin in the females of *Fundulus*
3. The marked intensification of coloration and iridescence in the males, both on the body and on certain fins.
4. The paling of color in the females.
5. Contact organs in spawning males.
6. The increased activity of the males, accompanied by an increase in courage.
7. The coyness of the females, especially in *Cyprinodon.*

All of these secondary sexual characters can, I believe, be shown to be either direct adaptations to the sexual life of the fish or necessary accompaniments of the high physiological tone that accompanies the sexual climax.

Of the permanent characters the most obviously adaptive are those that have to do with the differences in size of certain fins in the two sexes. Without reasonable doubt the enlarged dorsal, anal and ventrals are adaptations to facilitate clasping. The ori-

gin of this adaptation and the way in which it is thought to have given rise to the habit of intromission will be discussed later.

The differences in shape of certain fins may, with equal certainty, be said to be adaptive. The backwardly directed prolongations seen on the anal fins of all the species of *Fundulus* examined are evidently to give the male a greater reach in his effort to clasp firmly the body of the female. The shortness and softness of the dorsal fin of the female is of advantage in that it is thus less in the way.

Differences in color pattern can only be explained as sex recognition marks. It can readily be seen, in the light of the observations on the spawning behavior of these fish, that it must be possible for the males to recognize the females at once and at a distance. Some distinctive character that would appeal to the visual sense is required. In the course of evolution those females that could readily be recognized as females would be the ones most frequently mated with and they would be the most likely to transmit this variation to their descendants. There seem to be at least two means of acquiring a distinctive appearance that would serve to mark off the females from the males. One means is to lose the common racial marking more or less completely, and thus to acquire a sort of secondary solid coloration. This method can be seen in two stages of development in two species of *Fundulus*, viz., *F. diaphanus* and *heteroclitus*. The former presents a condition in which the bars of pigment of the female are simply narrowed markedly, while the latter shows their reduction to the merest suggestion of a cross-banded pattern. The second means of acquiring a distinctive female marking is exemplified by *F. majalis*, in which the characteristic banded pattern of the species, which is possessed by the young of both species, is, during ontogeny, gradually converted into a longitudinal striping of a most pronounced order. The stages in the process of change from a transverse to a longitudinal pattern have been described in another place.

Attention has been called to the sequence of changes from the young to the adult color pattern in both male and female of *Fundulus majalis*. In the first place there seems to be a very deep-seated law of antero-posterior development. In the second place

there is in the female a transition from a primitive cross-banded pattern to one characterized by longitudinal stripes. This is the opposite order of change from that given by Eimer and shows that his laws of orthogenetic variation have only a limited application. We have here a clear case of orthogenetic variation during ontogeny, a phenomenon that Gadow tried unsuccessfully to show in the case of scutes of *Chelonia*.

The total male plumage cannot be considered as primitive, the spawning plumage proper being secondary, an especial male acquisition due to his superabundant vitality. The cross-banded pattern is probably primitive and was possessed by both sexes. Even the distinct spot on the dorsal fin in the males of various species of *Fundulus* was probably a character common to both sexes, for in the allied species *Cyprinodon* we find this marking more pronounced in the female, but often present in rather vague form in the males.

Whether differences in the relative abundance of the sexes can be explained as adaptations is open to discussion. The fact that, in all the species studied, the males are relatively rare may be explained by the law of economy, for comparatively few males are quite capable of fecundating the eggs of many females, hence any more males would be superfluous. The experiment of putting too large a proportion of males in aquaria with females shows the disadvantage of a superfluity of males, for they spend most of their time fighting instead of devoting their attention to spawning.

The more slender body form of the males in *Fundulus* and the deeper but more compressed bodies of the males of *Cyprinodon* are probably both adaptions to the more active and combative disposition of that sex.

Of the temporary characters that accompany the sexual climax in both sexes, the heightened color of the males is most readily explained on purely physiological grounds. It is well known that heightened vigor, whether reproductive or somatic, is accompanied by a more active metabolism, and it is equally well known that pigmentation is a sort of index of the rate of metabolism in an organism. A heightened sexual vigor is then necessarily accompanied by an increase in pigmentation. So much for that

phase of color intensification that is simply dependent on an increase of pigment; the blue gleam that appears only during active spawning must be the direct result of sexual excitement, for it fades almost immediately when the males are removed from the sexual environment. I am inclined to look upon this gleam as a sort of flush such as might suffuse the human body under excitement.

Contact organs may be considered as excrescences produced by the excess vitality of the male and specialized for an especial function. As suggested in the introduction of this paper, it is believed that both structure and function appeared in response to a heightened metabolism. After their appearance the structures were modified by use or function.

It is interesting to endeavor to trace the origin and development of the habit of intromission that seems to prevail among about half of the Pœciliidæ. This habit is invariably associated with an increase in the length of the anterior rays of the anal fin and the modification of these rays in various ways into an organ of intromission. The first step in the process was doubtless a mere elongation of the whole anal fin, as seen in *Fundulus diaphanus*. The next step was probably a more rapid growth of the anterior rays of the fin, such as we see in *Fundulus heteroclitus* and to a slightly more marked extent in *Fundulus majalis*. The function of this elongation in these species of *Fundulus* is partially to give the male a greater reach and partly to fan the sperm toward the extruded eggs. It is only a few steps farther in the same direction for the anal fin to assist the sperm to enter the oviduct of the female when internal fertilization becomes necessary.

PLATE XXVII.

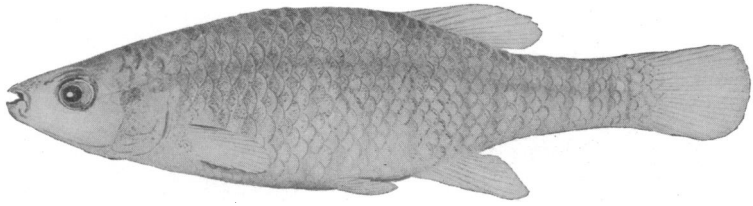
FIG. 1. *Fundulus heteroclitus*, female.

FIG. 2. *Fundulus heteroclitus*, male.

FIG. 3. *Fundulus majalis*, female.

FIG. 4. *Fundulus majalis*, male.

These figures and those in Plate XXVIII. are reproduced from wash drawings and represent the actual sizes of the average adults.



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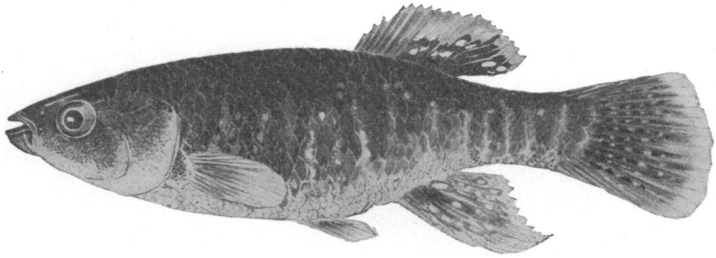

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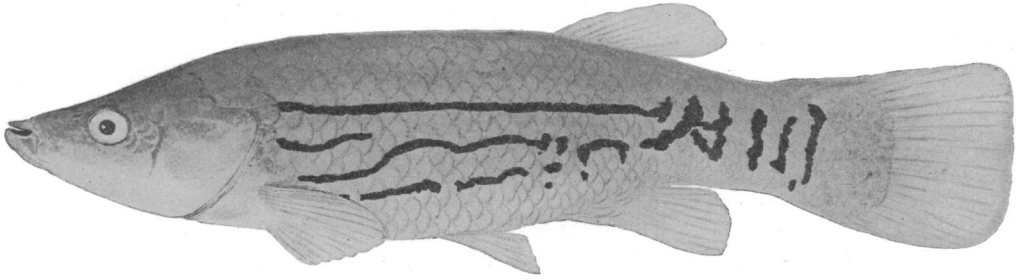

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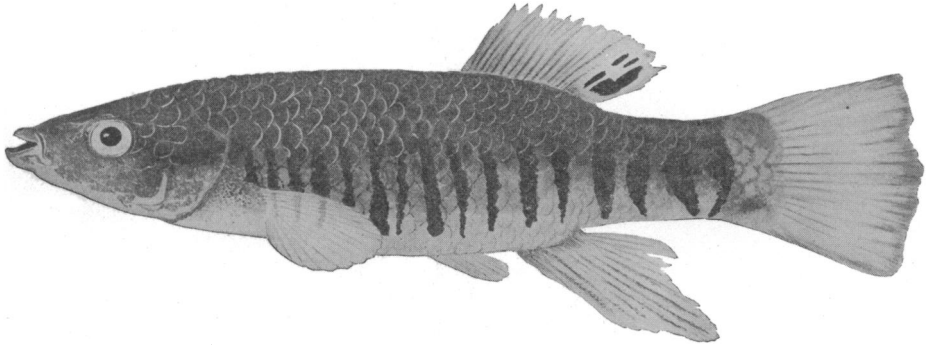

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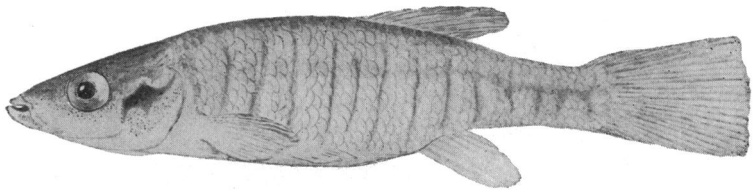
PLATE XXVIII.

FIG. 1. *Fundulus diaphanus*, female.
FIG. 2. *Fundulus diaphanus*, male.
FIG. 3. *Cyprinodon variegatus*, female.
FIG. 4. *Cyprinodon variegatus*, male.



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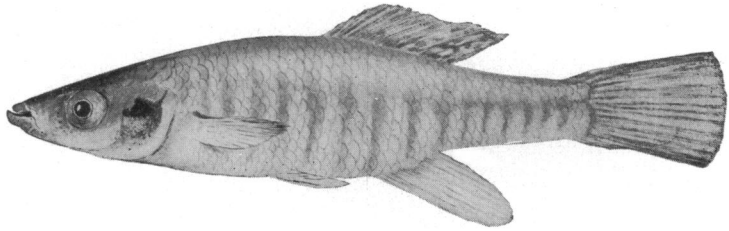

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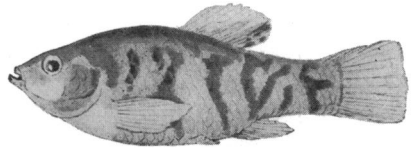

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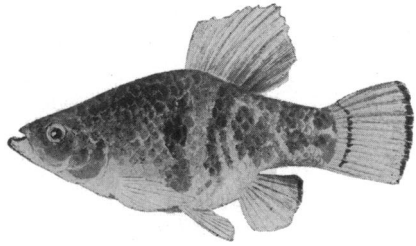

4